VARIATIONS IN CYTOLOGY AND GROSS MORPHOLOGY OF TARAXACUM

I. CYTOLOGY OF TARAXACUM LAEVIGATUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 293

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(WITH PLATES IX, X)

Introduction

These investigations are the outgrowth of a study, begun in 1914 at the instance of the late Professor C. E. BESSEY, of parthenogenesis in *Taraxacum vulgare* (Lam.) Schrk. and *T. laevigatum* (Willd.) DC. These two species are the common ones in central United States, being respectively designated as *Leontodon Taraxacum* L. and *L. erythrospermum* (Andrz.) by BRITTON and BROWN (3). In 1917 the existence of ameiotic parthenogenesis in both species was confirmed (23) and certain pollen abnormalities briefly described. These abnormalities have invited more critical analysis as a means of throwing light upon certain phases of variation and degeneracy, and likewise upon the problem of synapsis. The study of non-cytological variations has been directed largely to leaf characters. This is due to frequent references in the literature of *Taraxacum* to "polymorphy" and to the wholesale erection of species (cf. Index Kewensis 10).

Maturation phenomena in embryo sac and pollen have been homologized and found to be highly fluctuating. The fluctuations, instead of being anomalous, seem plainly to indicate variations in the duration and relative intensity of (1) chromosome individuality, (2) sex, (3) polarity.

Synapsis in the sense of chromosome pairing is expressed with varying degrees of vigor and quite without reference to doubleness of the spireme thread.

Leaf variation within the species is shown by quantitative studies to be a matter of senescence and rejuvenescence. The rôle of environment is secondary. The interplay of senescence and

environment is sufficiently potent to have produced from a few valid species transient forms fitting many published descriptions given specific or varietal rank. Attempts to correlate degree of leaf dissection with internal anatomy have not succeeded, but senescence and dissection are accompanied by an increase in carbohydrates as compared with nitrogenous substance.

Numerous colleagues, and in particular Professor JOHN H. SCHAFFNER of Ohio State University, have given generous help whenever called upon. It seems proper also to express appreciation of the difficulties confronting earlier workers whose conclusions, and in some cases whose observations, have not been confirmed here.

IDENTITY OF SPECIES.—This plant, known as the "red-seeded dandelion," is without doubt cosmopolitan. It is listed as *T. erythrospermum* Andrz. by GRAY (19), and as *Leontodon erythrospermum* (Andrz.) Britton by BRITTON and BROWN (3). SEARS (23), as well as SHERFF (25), for reasons that will appear later, has accepted the decision of HANDEL-MAZETTI (6) with respect to nomenclature.

BRITTON employs the generic name of *Leontodon* upon the authority of LINNAEUS' Sp. Pl. 798 (14). HANDEL-MAZETTI in his monograph presents the tabulation and critique of authorities upon which he bases his selection of the name *Taraxacum.* It is convincing. Incidentally he makes clear why *Leontodon Taraxacum* L. cannot stand as a valid species name because of incomplete diagnosis.

The species with which we are concerned here is discussed by the same authority as follows:

> Was den Namen anbelangt der bereits auf die diversisten Pflanzen angewendet wurde, so konnte ich mich an dem schön fruchtenden Originalexemplar Willdenows von seiner Bedeutung überzeugen. . . . . *Leontodon laevigatus* Willdenow, 1800; *Taraxacum laevigatum* De Candolle, 1813; *T. erythrospermum* Besser, 1822.

The last citation (quoted from the tabulation of synonyms on p. 109) is doubtless the one upon which GRAY and BRITTON base their specific nomenclature. BRITTON'S citation for the species is ANDRZEJOWSKY in Bess. Enum. Pl. Vilh. 75. 1821. For further critical discussion the careful paper by SHERFF (25) may be cited.

REPRODUCTION.—The more important studies of reproductive physiology and morphology in *Taraxacum* are so well known and so frequently cited that they require only brief comment here.

1896. SCHWERE (**22**): embryo arises from egg in sac of typical appearance.

1900. ANDERSSON and HESSELMAN (**1**): pollenless arctic specimens produce fruit, parthenogenesis suspected.

1903. RAUNKIAER (**18**): "Species Danicae Taraxaci castratione agamice propagari demonstratum est; species omnes Taraxaci semper parthenogenetice propagari verisimile est."

1904. KIRCHNER (**13**): pollen of *Taraxacum* never found germinating upon *Taraxacum* stigmas, although often abundant.

1904. MURBECK (**15**): confirms findings of SCHWERE, RAUNKIAER, and KIRCHNER. Finds embryos in unopened, pollenless flowers.

1904. JUEL (**11**): embryo sac maturation reduced to single division. Apparently no reduction, although prophase resembles heterotypic.

1905. JUEL (**12**): compares maturation phenomena of sexual *Chicoraceae* with those of *T. officinale* (*vulgare?*). Notes double thread in prophase of former but not in latter; former shows haploid number of bivalents in diakinesis, while *Taraxacum* shows diploid number (24–26) of univalents. These facts believed to favor the parasynaptic view of reduction. Following diakinesis in *Taraxacum*, nucleus is believed to elongate and chromosomes to split temporarily, the sequence being regarded as a shift from heterotypic to homotypic prophase. Pollen goes through reduction forming 12 or 13 bivalents in first prophase, but doubleness of spireme not observed.

1907. HANDEL-MAZETTI (**6**): noteworthy monograph of genus. Emphasizes genetic importance of parthenogenesis, but believes RAUNKIAER'S conclusion too sweeping. Shows clearly that pollen development must be highly variable.

1907. DAHLSTEDT (**4**): notes presence of numerous sterile seeds and surmises that normal eggs may be found in otherwise parthenogenetic heads. Also believes sexual species likely to exist.

1909. ROSENBERG (**20**): compares chromosome conditions of *T. officinale* (*vulgare?*) and *T. confertum*, finding in the latter a typical reduction from 16 to 8.

1910. IKENO (**9**): reports *T. platycarpum* Dahlst. to be sexual, while *T. albidum* Dahlst. (white-flowered) is not.

1912. SCHORBATOW (**21**): confirms previous findings for *T. officinale* Wigg. Takes liberal cognizance of cytological variation.

1913. OSAWA (**17**): compares in detail cytology of species studied by IKENO, agreeing in general with JUEL's conclusions. Finds a variable degree of pairing in pollen diakinesis of *T. albidum*, and besides normal maturation of tetrads, the formation of diads by "homotypic" division. Notes amitosis and supernumerary nuclei in pollen; also 16 and 8 chromosomes in sexual, 36 to 40 in parthenogenetic species. Parthenogenesis probably due to hybridization.

1917. SEARS (**23**): *T. laevigatum* as well as *T. vulgare* shows ameiotic parthenogenesis. The former generally gives higher percentage of sterile fruits, and both exhibit pollen abnormalities, including extrusion of chromatin, amitosis, and defective spindles.

1920. STORK (**26**): *T. laevigatum* is ooapogamous, and embryo sac maturation agrees in general with accounts of JUEL and OSAWA for other ooapogamous forms. Also 26 to 30 chromosomes found, but said not to split during the elongated phase which is believed to follow diakinesis.

RELEVANT CYTOLOGICAL PROBLEMS.—As suggested earlier, those of chief interest in connection with the present study are (1) the mode of synaptic pairing, and (2) cytological variation.

SYNAPSIS.—The conclusion of workers already quoted (**12, 17**), who have compared ameiotic species of *Taraxacum* with related sexual species, favors the parasynaptic interpretation of reduction division. Such conclusion is doubtless justified if the observations of prophase conditions upon which it is based are unexceptionable.

The development of thought upon the subject of synaptic pairing has been fully treated by numerous workers, the present trends of botanical opinion being fairly crystallized in papers by DIGBY (**5**) and SHARP (**24**). It is unfortunately true that various questions involved hinge upon observations made near the limit

of resolving power of the microscope. This introduces what should frankly be recognized as a potential source of error, and dealt with accordingly. In undertaking this study it was hoped that the more obvious sequence of events in a parthenogenetic plant might afford a check upon observations necessarily made under conditions of optical difficulty. This hope has at least been partially justified.

VARIATION IN CELL PROCESSES.—Cytologists have, through no fault of judgment, been so charged with the duty of learning the normal sequence of events in plants that as a rule they have given little attention to "anomalies." Even the most conservative theories of the cell as a physico-chemical mechanism must admit the likelihood of considerable fluctuation in its processes. WASIELEWSKI (**27**) emphasizes the phylogenetic continuity between mitosis and the types of amitosis produced by chloroforming meristem. Moreover, the results obtained by NATHANSOHN (**16**) in producing abnormal division types by the use of ether are highly suggestive, when viewed either in the light of modern theories of anaesthesia or of such work as that of BONNS (**2**). The latter has clearly shown a marked increase in proteolytic enzyme activity as a result of etherization. The experiments of HOTTES (**8**), demonstrating powerful effects of temperature change upon the spindle mechanism, are likewise significant. They become peculiarly so in connection with the intimate relation of temperature to enzyme activity.

Careful study and classification of variations in cell behavior have already yielded data of interest in genetics, and they may afford the clue to an isolation and analysis of the factors involved in cell behavior, which are now known, so far as they are recognized, by terms so general as to be noncommittal.

Procedure

All material studied was collected from plants which had been identified after fruiting. A wide range of fixing reagents was tested, including mixtures of absolute alcohol and glacial acetic acid in various proportions. The best results were obtained with a solution of two parts of alcohol and one of acid. Beautiful

preparations were obtained by the use of Flemming's stronger fixing fluid. In comparison with acetic alcohol material these showed little difference in nuclear condition, but inspection of the cytoplasm made it very evident that the electrolytes contained in Flemming's solution had caused violent coagulation of certain cell colloids. This circumstance should militate against its use in critical work. Acetic alcohol kills almost instantly, and contains two components whose effects are mutually corrective. From the theoretical standpoint of modern colloid chemistry it ought to be a very desirable reagent. Numerous experiments, as well as the variety of formulae which have been recommended by different workers, suggest strongly that failures with it have often been due to use of unsuitable proportions of the components.

Sections were cut from 6 to 12 μ in thickness, and were stained with iron-alum, alone and with counterstain, and with Flemming's triple solution. Drawings, unless otherwise noted, were made with Spencer camera lucida through Bausch and Lomb binocular equipped with no. 12 compensating oculars and 1.9 fluorite objective.

It should be noted that the use of the word synapsis in this paper has been limited to the matter of synaptic pairing. The term synizesis is used throughout to designate the balling of chromatin in early prophase.

Observations

SOMATIC DIVISIONS.—These were observed very frequently in all stages, in nucellar and other meristem. So far as can be determined, they present no unusual features. The chromosomes segment as curved rods from a fairly thick and quite uniform spireme, and are certainly about twenty-six in number.

MATURATION DIVISIONS.—The earliest stages that could be identified were marked by an enlarged nucleolus and not more than thirteen paired centers of chromatin aggregation. These are shown in figs. 1 and 2, and can fairly be construed as prochromosomes. JUEL (12) does not mention them, while OSAWA (17) describes them for both the species he studied as originating by an increase in size and number of the granules upon a linin meshwork,

that is, from a resting nucleus as conventionally described. Observations here lead to agreement with SHARP (**24**), as follows:

> While one easily gains the impression of separate chromatin granules connected by threads with another substance . . . . it seems more probable that the "chromatin granules" are merely the heavier portions of the alveolated and reticulated chromosomes, and that the lighter "supporting network" consists simply of the thinner portions of the same, together with the delicate anastamoses.

In portions of the thread as it enters synizesis, a curious partly paired, partly vacuolate-split appearance is discernible (fig. 3). It is stages of this sort which lend themselves as conveniently to one philosophy of nuclear division as another, and which should not be taken as pivotal until all other means of explanation have been exhausted. The optical difficulties attendant upon the close state of aggregation are very great here of course, necessitating thin sections and special technique.

Synizesis culminates in an extremely dense ball whose components are without doubt filiform. The embryo sac mother nucleus in fig. 4 is typical in every respect save that of size, being larger than usual. The loosening thread (dolichoneme) is fairly uniform at first (figs. 5, 6), and JUEL (**12**) is doubtless right in stating that any apparent nodes are optical effects due to foreshortening or crossing.

After the thread becomes rather evenly distributed through the nuclear cavity, its uniform appearance is altered by the advent of changes which are hard to explain except as fissions. Certainly they are quite different from (1) accidental or other juxtaposition of whole threads, or (2) the twisting together of limb and bight into a loop. Both (1) and (2) are to be seen in figs. 7 and 8, where they may be compared with the seeming fissions. Whatever the change that gives this appearance of duality, it is clearly not simultaneous throughout the thread. A priori, is there any reason why it should be? The unevenness of its origin perhaps may explain the failure of other students of parthenogenetic species of *Taraxacum* to observe anything suggesting a "double" thread. Careful inspection of OSAWA'S fig. 46 (**17**) shows that the phenomenon is by no means precluded there.

Instead of occurring uniformly, thickening of the thread seems to be accompanied by the beginnings of its segmentation. Figs. 9 and 10 show nodes whose structure is seemingly homogeneous. On the other hand, it is always possible to find some showing clearly a longitudinal duality, even culminating in a divergence or forking of the two attenuate ends. If this appearance of doubleness were visible in every node and the divergent internodes were not visible, one would be justified in seriously questioning the validity of the interpretation. It might then be simply the lateral shadowing normal to translucent cylindrical bodies. If, however, there is really duality, the separating plane in certain nodes must lie more or less parallel to the section and hence not be visible. This would account for those nodes whose appearance is homogeneous.

The nodes rapidly shorten and become truly homogeneous, only the bifurcate internodes remaining as evidence of the double origin of each chromosome. As in all chromosomes, there are occasional lateral projections in addition to the forking internodes, due doubtless to imperfect retraction of pseudopodia at some time during aggregation. The papers already cited (**12, 17, 26**) evince little proof of close attention to this stage, a circumstance doubtless due to its transient character. Figs. 11–13*b* show it in varying aspects. Fig. 12 suggests a rough correspondence between this phase and the so-called second contraction. Certainly the thread shortens greatly, and the chromosomes as they first cut apart are no longer peripheral, but in the nuclear interior.

The bifurcations at each end of the chromosome are not retracted at once, but may shift slightly in position. This gives the appearance of pseudopodia, generally four in number. STORK, OSAWA, and JUEL have all more or less plainly figured but not accounted for these pseudopodia. Fig. 14*b*, as those of the authors cited, shows that after the chromosomes drift to the nuclear membrane and become peripherally oriented, the quadruple projections tend to move to the side of the chromosome away from the membrane. These, with other irregular projections of earlier or later origin, may constitute the "fringe" referred to by JUEL and figured by OSAWA.

Counts at this stage, and also at the somewhat later one resembling diakinesis, show twenty-six chromosomes. This agrees

with JUEL'S (12) counts for *T. officinale*. The count registered by STORK for the species now under discussion is twenty-six to thirty. Since the latter takes no cognizance of fission at any time before metaphase, it is possible that his higher estimate is due to reckoning separated halves as units. It will be recalled that the somatic number is about twenty-six, and that there are about thirteen pairs of prochromosomes. Fig. 22 shows a normal reduction division of thirteen univalents at the homotypic plate. These facts all give the necessary assurance that in prophase we have the origin of the diploid number of univalents, unpaired, from a dual and therefore a split thread.

To summarize developments thus far, there is first the appearance of approximately thirteen (the haploid number) pairs of prochromosomes. The thread entering synizesis shows in places a doubleness unexplainable at present. The thread emerging from synizesis becomes very evenly distributed through the nucleus, and then shows what is interpreted as non-simultaneous splitting. By the time segmentation is reached splitting becomes indubitable, and the formation of twenty-six univalent chromosomes occurs by the lateral refusion of the two halves previously split apart.

In contrast with these findings it should be noted that JUEL, OSAWA, and STORK, working on parthenogenetic species of *Taraxacum*, all expressly state that the postsynizetic thread is single and remains so, and that the univalent chromosomes are single in composition. JUEL and OSAWA, working on sexual plants of the same or nearly related genera, report an obvious doubleness of the thread. Since there is no question of the duplex nature of bivalent chromosomes in sexual plants, these investigators conclude that the doubleness noted is due to synaptic pairing. The three workers cited agree that diakinesis is followed by the greatly elongated nucleus as mentioned. STORK, however, considers the chromosomes here to be unpaired, that is, unsplit because "there are certainly not upward of sixty." Accepting his maximum count of thirty as correct, one would scarcely expect to find more than sixty halves.

Comparison of figs. 12–15 with figs. 36–41 strongly suggests that the elongated nucleus is not the outcome of diakinesis, but a

divergent form of it. The chromosome forms in the two sets of figures show no interrelation, but a common origin at segmentation.

It will particularly be noted that connections between chromosomes persist in the beginnings of the elongated stage but not in diakinesis, making it quite unlikely that the former is a derivative of the latter, but not militating against the idea that both are derivable from late segmentation.

The nucleus in the elongated stage is often lobed, moreover, as in fig. 40, and constricted and binucleolate as in fig. 41. In short, the elongated nucleus with about twenty-six *X* and *Y*-shaped chromosomes must be regarded as part of a distinct sequence

TABLE I

Stage	Sequence *A*	Sequence *B*	Sequence *C*	Sequence *D*
Prochromosome	13 pairs	13 pairs	13 pairs	13 pairs
Synizesis	Normal	Normal	Normal	Normal
Loose skein	Normal	Normal	Normal	Normal
Splitting	Visible	Visible	Visible	Visible
Segmentation	26 cuboids	26 cuboids	26 cuboids	26 *X*'s and *Y*'s; nucleus long
Synapsis	Prompt	Slow	Slow or none; nucleus long	None
Orientation	Compact	Loose	Irregular	None; nucleus lobing
Spindle	Fibers to bivalents	Fibers to univalents	Defective	None
Metaphase	Qualitative, narrow	Quantitative, broad	None or very irregular	Amitosis
Second division	Quantitative, homotypic	Quantitative, somatic (or none)	None, irregular or amitotic	None or amitotic

arising from segmentation and culminating in amitosis, and not as a curious step in the normal maturation process. This amitotic type of development may be designated as sequence *D* (table I). It is illustrated in figs. 36–42.

Returning to diakinesis with its twenty-six cuboid chromosomes, this stage may develop further in any one of the three ways outlined in table I, and designated as sequences *A*, *B*, and *C* respectively. Type *A* is illustrated in figs. 16–22. Here pairing is end to end, following diakinesis, and is both prompt and complete. Orientation is uniform and compact, resulting in a heterotypic metaphase

with thirteen bivalents. This sequence has been completely followed in pollen through heterotypic mitosis and the ensuing homotypic division where (fig. 22) thirteen univalents show. In the embryo sac it has only been traced with definiteness through the compact orientation stage (fig. 17), while fig. 21*a*, *b* represents a badly masked anaphase showing thirteen chromosomes at each pole. In addition, it is likely that the metaphase shown by STORK in his fig. 16 is heterotypic, since it agrees with the general aspect of such a stage as found frequently in pollen. Whether the second (quantitative or homotypic division) can occur in the embryo sac as it does in the pollen maturation, giving true reduction, is not known. Inspection of hundreds of embryo sacs failed to disclose tetrad formation, and yet the large numbers of empty fruits in *T. laevigatum* may eventually be explained by occurrence of reduced embryo sacs, never fertilized, quite as much as by the occurrence of amitosis of sequence *D*.

Sequence *B* is shown in figs. 23–30*b*. It is ostensibly the sequence which results in reproduction, inasmuch as it is the only mechanism found which in the absence of fertilization insures preservation of the constant chromosome equipment characterizing the species. In this sequence the nuclear membrane disappears before synapsis and orientation are complete. Synaptic pairing is end to end, but takes place so slowly that spindle fibers become attached to each of the halves of each univalent instead of to the univalent as a whole. In consequence the pairs come to metaphase thirteen in number, but with components still end to end and transversely oriented. The resulting spindle (figs. 27, 28) is much broader than that of sequence *A*, and the division is quantitative instead of qualitative, if ordinary canons be right. The partial or delayed pairing here was noted by OSAWA in the pollen of *T. albidum* only, did not attract the attention of STORK, and seems to have been interpreted by JUEL (12) as a splitting. HOGBEN (7) has described similar phenomena (delayed synapses) in parthenogenetic animals, while the present observations are amply verified by numerous counts made throughout the sequence. Sequence *B* in pollen seems to result in diads of fairly uniform nature, which as a rule do not undergo further growth. In the embryo sac it likewise

produces a diad. One of the cells, usually the apical, disintegrates, while the other develops into an eight-nucleate sac by regular vegetative mitoses. A prophase of the first of these mitoses is shown in fig. 30*a*, *b*, with twenty-six somatic chromosomes segmented.

Sequence *C* is illustrated in figs. 31–35. It comprises a rather wide range of gradations in behavior, completely bridging the gap between types *B* and *D*. Following segmentation, the nucleus elongates, and the membrane disappears, with the twenty-six cuboids widely scattered and quite unpaired. As the spindle fibers appear, orientation and pairing are quite variable in their degree of perfection. In fig. 32 spindle, synapsis, and orientation seem rather perfect, excepting that chromosomes from the extreme ends of the nucleus have been caught at the poles and will doubtless remain there. In other cases pairing cannot be detected, and the majority of the cuboids may be caught at the poles, only a few or none reaching metaphase position. These latter constitute the "delayed" chromosomes familiar in descriptions of pollen abnormalities, although actually the lagging ones are those at the ends. Obviously it is but a short step from this condition, where no cuboids reach metaphase, to amitosis as already described for sequence *D*.

Sequence *C* is best exemplified in the pollen. In the embryo sac it has been traced through orientation. With amitosis it shares most of the responsibility for pollen abnormalities recorded in a previous paper. The chromosomes which never reach metaphase position are likely to be reorganized into nuclei before those at the center reach the poles. These latter "delayed" chromosomes then reorganize as supernumerary nuclei. Additional causes of supernumerary nuclei are (1) irregular lobing during first amitosis, (2) a second amitotic division, (3) extrusion of chromosome substance and formation of membranes about it.

It should be understood that the four sequences described intergrade almost insensibly. It should also be noted that sequence *D* in its extremest fluctuations shows nuclear elongation and amitosis beginning so soon after synizesis that the chromatin has no opportunity to organize beyond the condition of a granular thread.

Discussion

The more important implications of these findings fall under (1) relation to previous hypotheses explaining maturation in parthenogenetic species of *Taraxacum;* (2) effect upon interpretations of normal reduction division (particularly as to synapsis) which have been based upon comparisons of sexual and parthenogenetic species of *Taraxacum;* (3) elucidation of the findings themselves in terms of the fundamental cell activities involved.

1. JUEL'S (12) hypothesis, accepted in more or less modified form by subsequent workers, is that maturation in *Taraxacum officinale* begins as a heterotypic and shifts to a homotypic division. As previously stated, this is based upon his belief that the elongated nucleus with *X*-shaped chromosomes follows diakinesis and precedes spindle formation. Since, as has been indicated, the elongated nucleus is a member of a distinct sequence, the hypothesis is placed upon the defensive. Barring this discrepancy, however, the type of division described by JUEL is essentially that of sequence *B*, the type effective in reproduction. It might appear that this is virtually homotypic, since quantitative, and therefore mainly if not in detail in agreement with JUEL'S theory. Possibly this is true, but number and character of chromosomes do not correspond with those usual in homotypic divisions. Sex as a factor is completely absent in homotypic division, while here it is present, in abeyance of course, but potential. This is evidenced by (*a*) chromosome number, (*b*) pairing of prochromosomes, (*c*) synaptic pairing (albeit delayed) of the cuboids, (*d*) occasional cases of true reduction in pollen and presumably in embryo sac. It seems, therefore, that the designation "ameiosis," or "amiosis," proposed by SEARS in 1917 (23), and indicating a type of maturation which obviates necessity for subsequent fertilization, is to be preferred to "homotypic mitosis," a term of very explicit implications.

2. The parasynaptic interpretation of reduction division, so far as normal sexual species of *Taraxacum* are concerned, was favored by the work of JUEL and OSAWA, since both workers noted a duality of spireme thread in meiotic and none in ameiotic plants. Closer scrutiny previous to segmentation has revealed a duality in the segmenting thread, while precise counts have indicated that this

duality represents a splitting and not a pairing. These facts seem sufficient to warrant more critical comparison of prophases in sexual and parthenogenetic species of *Taraxacum* before deciding that parasynapsis is actually the source of duality in spireme threads of the former. Moreover, the completed synapsis in sequence *A*, as well as the delayed pairing in sequence *B*, is end to end, rendering any assumptions still more difficult.

3. We have seen that ameiosis does not involve the complete elimination of sex. Rather it involves a retardation and partial inhibition of sex expression. The least degree of inhibition gives us sequence *A*, practically a normal reduction division with synaptic mates pairing only a little more slowly than is usually the case. A greater degree of inhibition obviously occurs in sequence *B*, the delay being more marked. Whatever the ultimate cause of such delay, there can be no question that it amounts to a persistence of chromosome individuality, which at segmentation supersedes the individuality of the nucleus as a dominant phase. The nature of sex inhibition in sequence *C* is more complex. Synapsis is slow and of varying perfection. It is marked by an elongation of the nucleus, clearly indicating a premature expression of polarity. We may conclude, therefore, that encroachment upon sex is progressively increasing.

Type *D* is readily interpreted, in view of these intermediate conditions, as the still earlier and more powerful expression of polarity at the segmentation stage. Not only does the nucleus become greatly elongated and eventually pulled apart, but the spireme split begun in prophase is never even temporarily overcome by the forces making for chromosome individuality. This is evidenced by the presence of *X* and *Y* forms, already noted. Such interpretation of the amitosis in sequence *D* by no means vitiates any possibility that it may be a matter of emulsification, as suggested by coupling the work of NATHANSOHN and that of BONNS. It merely involves a third, and not unreasonable factor, enzyme action, as a means of upsetting the delicate balance between the forces which we ignorantly know as individuality, polarity, and sex. That the dominance of polarity is not likely to be perfect seems probable from the nature of the factors which it overrides.

We have therefore a theoretical right to expect such phenomena as chromatin extrusion, irregular lobing, etc. The supernumerary nuclei produced by such means are thus quite a secondary phase of pollen degeneracy.

Summary

1. Maturation in *Taraxacum laevigatum* differs from that previously described for parthenogenetic species of *Taraxacum* in early prophase, chiefly by showing a split thread from which twenty-six univalent chromosomes segment.

2. Following segmentation, there may be any of four intergrading sequences instead of a single uniform sequence as described for other parthenogenetic species of *Taraxacum*.

3. These sequences are: *A*, almost typical reduction division characterized by perfect end to end pairing of the univalents; *B*, a qualitative division resulting in diads from which the functional embryo sacs arise and for which the term "ameiosis" is proposed, and in which sequence the univalents are slow in pairing; *C*, a more or less irregular division in which pairing of univalents is variable, accompanied by premature elongation of the nucleus and defective orientation; *D*, amitosis in which the nucleus elongates very prematurely and the split thread persists after segmentation, giving twenty-six *X* and *Y*-shaped chromosomes. There is no spindle.

4. These variations are not anomalous, but are traced to an increasing degree of inhibition of sex by other forces, to wit, chromosome individuality and polarity.

5. JUEL'S (12) interpretation of maturation in *T. officinale*, that it begins as heterotypic and switches to homotypic, does not apply in the present case.

6. Evidence for parasynapsis in Chicoraceae, so far as predicated upon the presence of a dual thread only in sexual species, must be reexamined.

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EXPLANATION OF PLATES IX AND X

All figures show a magnification of about 1600, excepting fig. 25, which is about 1200.

FIG. 1.—Complete view of very early E.S.M.C., showing about thirteen paired centers of chromatin aggregation.

FIG. 2.—Partial view of similar nucleus.

FIG. 3.—E.S.M. nucleus entering synizesis, showing curious partly paired, partly vacuolate appearance of chromatin masses.

FIG. 4.—Unusually large E.S.M.C. at climax of synizesis.

FIG. 5.—E.S.M.C. emerging from synizesis, showing uniform character of thread.

FIG. 6.—The same, somewhat later.

FIG. 7.—The same, thread becoming less homogeneous.

FIG. 8.—The same, thread showing dual character in places.

FIG. 9.—The same, segmentation beginning, thread thicker and dual character obvious in most nodes.

FIG. 10.—P.M.C. showing segmentation and dual nodes.

FIG. 11.—E.S.M.C., chromosomes becoming homogeneous, duality mainly visible at internodes.

FIG. 12.—The same, showing origin of cuboid chromosome form; thickening of thread producing contraction of mass toward center.

FIGS. 13*a*, *b*.—Complementary sections of same E.S.M. nucleus, with twenty-six (diploid number) chromosomes, cuboid and with traces of dual internodes still showing.

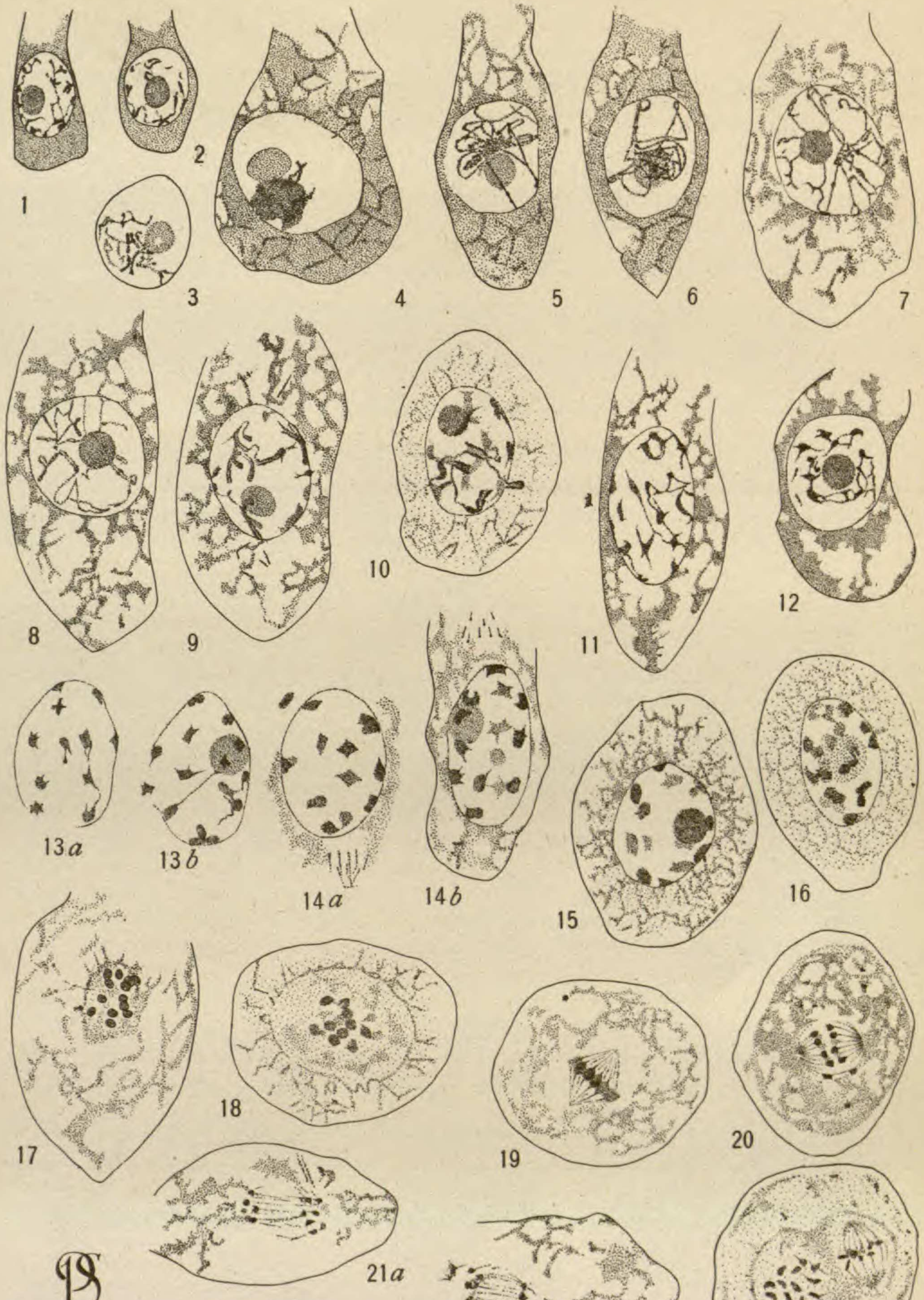
FIGS. 14*a*, *b*.—The same, somewhat later, showing various retractions and shiftings of quadruple internodal traces.

FIG. 15.—Part of P.M.C. at same stage as preceding.

FIG. 16.—Complete P.M.C., showing beginning of end to end synaptic pairing of twenty-six univalent cuboids.

FIG. 17.—Late orientation stage in sequence *A*, E.S.M.C. showing synapsis completed.

FIG. 18.—Same for P.M.C.



SEARS on TARAXACUM